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HYBRIDIZATION IN NATURE BETWEEN SPECIES OF AMERICAN CYPRINODONT FISHES

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INTRODUCTION

THIS study is one of a series, in which an attempt is being made to analyze the hybridization in nature between species of fish. The aims and methods presented in the recent papers by Hubbs and Kuronuma (1942) and by Hubbs, Hubbs, and Johnson (1943) have been followed. Pertinent literature references are included in those papers.

Two of the three hybrid combinations described on the following pages are treated as intergeneric. In all three sets the parental forms are undoubtedly very well-marked species, but whether any or all should be treated as generically distinct is a matter of taxonomic judgment. Until recently, in fact, both members of each parental pair now regarded as generically distinct were customarily referred to a single genus. Thus *Chriopeops goodei* and *Lucania parva* were both classed in *Lucania*, and *Plancterus kansae* as well as *Fundulus sciadicus* were both put in *Fundulus*, by Jordan and Evermann (1896: 632-66; and 1898: 2828) and by other authors. The discovery of new characters, along with a different interpretation of long-known features, has led recent revisers of the Cyprinodontidae to treat *Chriopeops* as generically distinct from *Lucania*, and *Plancterus* as separable from *Fundulus* (Myers, 1924: 8; 1925: 370; and 1931: 10; Hubbs, 1926: 5, 14).

Until the specimens here discussed were discovered, we knew of no natural hybrids in the oviparous cyprinodonts. We had already become convinced that Weed (1921: 70) was in error in reporting an extensive local hybridization between three species of *Fundulus*. His remarks were as follows:

. . . Under certain conditions hybridization in nature is very common.

The writer once found in some pools near Chesapeake Beach, Maryland, very large numbers of three species of *Fundulus* breeding in very restricted waters. Hundreds, if not thousands of fish were emitting spawn and milt at the same time in a space of not much over a hundred square feet of water a few inches deep. About half of the fish taken in those pools showed such intergrading characters that they could not be identified.

It seemed inherently improbable that three species would engage in such promiscuous spawning, and no other natural hybrids in *Fundulus* were known. The senior writer therefore undertook to check the case. Mr. Weed kindly furnished the information that representative specimens had been left at the United States National Museum. A search there, among uncatalogued as well as catalogued specimens of the three species of *Fundulus* involved (*F. diaphanus*, *F. majalis*, and *F. heteroclitus*), disclosed much material collected by Mr. Weed near Chesapeake Beach, but failed to uncover a single apparent hybrid. Field collecting, in localities said by Earl D. Reid to be the places where Mr. Weed seined, yielded an abundance of the three forms just named. After due allowance was made for age and sex differences, every fish could be identified, as one of the three species rather than as a hybrid. We now report, however, one hybrid between *F. diaphanus* and *F. heteroclitus*.

Incidentally, the similar mass hybridization between "*Notropis heterodon*, *Notropis cayuga*, *Notropis anogenus*, etc.," indicated by Weed (1921: 69-70) as probably occurring in Turtle Creek, Wisconsin, and in Lake Ontario, failed of confirmation when the material was re-examined. The difficulty with the Wisconsin collection lay largely in the inclusion of a form, *Notropis xanocephalus richardsoni* (Hubbs and Greene), which was unknown in 1921.

Natural hybrids, however, are known to occur in the Poeciliidae, a family of viviparous cyprinodonts (Hubbs and Hubbs, 1932; Hubbs, 1933; and 1936: 245-46, Pl. 8, Fig. 4). Hybridization in this family is being subjected to an extensive experimental study, with results that have recently been summarized (Hubbs, 1940: 205-9).

The single hybrid between *Fundulus diaphanus diaphanus* and *Fundulus heteroclitus macrolepidotus* was found in a large collection from Prince Edward Island, sent to us by M. W. Smith of the Fisheries Research Board of Canada. It came to light after this paper had been written. The *Chriopeops* × *Lucania* hybrids were discovered by Boyd W. Walker, who made the counts and measurements for this combination. The specimens were collected in Florida by Carl L. Hubbs, Laura C. Hubbs, and Boyd W. Walker. The *Fundulus* × *Plancterus* cross was found by Raymond E. Johnson in the course of his survey of the fish fauna of Nebraska, and he made the comparison between the single known hybrid specimen and the parental species.

All specimens used in this study are deposited in the fish collection of the University of Michigan Museum of Zoology.

The methods of counting and measuring follow those outlined by Hubbs and Lagler (1941: 12-20, Figs. 2-3). As in two previous papers, by Hubbs and Kuronuma (1942: 291-94) and by Hubbs, Hubbs, and Johnson (1943: 6-8), we find it very useful to compute a hybrid index, for each character of each specimen. This index denotes the position of the hybrid between the parental species, on a percentage scale in which the average value for the more primitive parental kind is set at 0 and that for the other form at 100. In the present study *Fundulus diaphanus* is interpreted as less specialized than *Fundulus heteroclitus*; *Chriopeops* as more primitive than *Lucania*; *Plancterus* as a derivative of *Fundulus*. The several hybrid indices of all specimens are averaged for each character, and all the character indices for each fish are averaged for each individual. A grand average is then obtained, to indicate the relations of all the hybrids to the parental species in all characters that were counted and measured.

Some characters that were counted and measured have not been tabulated. The data were discarded when no significant difference between the parental species was indicated, or when the ranges of variation for the two parental species overlapped very widely and the difference between the hybrids and either parental type was much less than the range of variation for either parent.

Fundulus diaphanus diaphanus $\times$ *Fundulus heteroclitus macrolepidotus*
(Pls. I-III)

U.M.M.Z. No. 138833: 1 adult female discovered in a large collection of *Fundulus* seined by M. W. Smith of the Fisheries Research Board of Canada on the shoals of Lake of Shining Waters, on Prince Edward Island, in the Gulf of St. Lawrence, on August 23, 1939.

Dr. Smith informs us that this is a fresh-water lake with a pH of 8.9 at the time and place of collecting; water temperatures ran from 17.5° to 26.6° C.; emergent and submerged vegetation grew plentifully, and the shores were also vegetated.

Concerning the ecology of Lake of Shining Waters and other "ponds" on Prince Edward Island in which large samples of *Fundulus* were taken in a fishery biology survey, Dr. Smith supplies further information, as follows. All the lakes lie just behind the mouths of small streams, back of barriers built up above high tide level. Salt water does not spill into these ponds at the normal high tide, but in times of storm varying amounts of sea water may wash in. Records for Clark Pond indicate a variation in salinity from 0.7 to 22.2 parts per mille. Dalvay, Long, and Shining Waters are virtually fresh-water habitats, and have been found to contain only traces of salt water, although it is known that the latter 2 ponds have at times been flooded. The areas and maximum depths are: Lake of Shining Waters, 8.1 hectares, 2.2 meters; Clark Pond, 12.1 hectares, 3.0 meters; Long Pond, 19.8 hectares, 2.0 meters; Dalvay Pond, 22.1 hectares, 3.7 meters. Aquatic vegetation is plentiful in all the ponds—*Sparganium* and *Typha* along the

shores, and *Potamogeton* and *Myriophyllum* in extensive beds within the water. In the ponds other than Lake of Shining Waters the temperatures at the time of collecting ranged from 22.2° to 25.5° C., and the pH from 8.4 to 9.0. All series were taken August 23, 1939. All of the collections were made with a seine and were entirely random in regard to the species of *Fundulus*. In fact, it was not recognized in the field that 2 species (and the 1 hybrid) were included. It is clear, therefore, that *Fundulus diaphanus diaphanus* was the dominant form of the genus, and very abundant, whereas the essentially salt- and brackish-water *Fundulus heteroclitus macrolepidotus* was very scarce (Table I).

The lakes of Prince Edward Island are obviously *diaphanus* habitats, into which a small number of the bay-shore form *heteroclitus* has wandered.

TABLE I
RELATIVE NUMBERS OF HYBRIDS, *Fundulus diaphanus diaphanus* × *Fundulus heteroclitus macrolepidotus*, AND OF THE PARENTAL SPECIES, IN COLLECTIONS
FROM THE LAKES OF PRINCE EDWARD ISLAND

Lake	<i>Fundulus diaphanus diaphanus</i>	Hybrids	<i>Fundulus heteroclitus macrolepidotus</i>
Lake of Shining Waters	637 (97.5%)	1 (0.2%)	15 (2.3%)
Clark Pond	262		36
Long Pond	2295		9
Dalvay Pond	616		
In all 4 collections	3810 (98.4%)	1 (0.03%)	60 (1.6%)

The unusually robust form of the males in these collections of *Fundulus diaphanus diaphanus*¹ suggested to Dr. Smith that there might have been some hybridization in the Prince Edward Island lakes between *F. diaphanus* and *F. heteroclitus*. We were unable to verify the suspicion that this character was due to hybridization, but on carefully examining the 4 large series we did locate the 1 hybrid. Its status can hardly be open to question, for it is thoroughly different from and definitely intermediate between the 2 assumed parental species. No other cyprinodont ranges into the Maritime Provinces.

This single hybrid specimen is intermediate in color tone, coloration, general body form, and proportions; in the gillraker, scale, and fin-ray numbers; and in certain superficial structures. The characters subjected to statistical treatment bring out precisely the intermediacy of the hybrid (Table II). The grand average hybrid index for the characters analyzed in Table II is 50, indicating that in these respects the hybrid is on the average exactly intermediate between the parental species.

¹ The subspecific characters of *Fundulus diaphanus diaphanus* have been stated by Hubbs and Lagler (1941: 67).

In all the proportionate measurements the values for the hybrid lie between those for the parental types. There is no overlap for 11 items (body and caudal peduncle depths, predorsal and prepelvic lengths, height of anal sheath, head depth and width, interorbital and mouth widths, diameter of nonimbricated scale, and 1 of the pore measurements). The position of the dorsal fin (Pl. I) is a particularly obvious character of the hybrid: when measured forward the distance from the caudal base to the origin of the dorsal fin extends to the posterior part of the eye in *F. d. diaphanus* (to the posterior margin of the orbit in 1), to just behind the eye in the hybrid, and to about the middle of the opercle in *F. heteroclitus macrolepidotus*. The hybrid value is also intermediate, but shows a slight overlap on the measurements of one or both parental species, in 6 characters (length of depressed dorsal fin, of snout, and of orbit, upper lip width, and 2 of the pore measurements). The character index based on the 3 pore measurements (Pl. III), however, intervenes, with a wide gap on either side. The pattern formed by the canals and pores on the top of the head is one of the clearly intermediate characters. The ratio of the head depth to orbit length in the hybrid is distinctive, without overlap. The angle between the head contours barely overlaps the values for *F. d. diaphanus*. The displacement index, measuring the obviously different relative bulks of the bodies (all eviscerated), is interpolated between the ranges for the parental species, without overlap, though *diaphanus* is approached more closely than is *heteroclitus* in this respect.

The intermediacy of the hybrid is confirmed by the gillraker, scale, and ray counts. The raker counts are 5 to 7, usually 6 for *diaphanus*, 8 for the hybrid, and 9 to 12 for *heteroclitus*. The number of transverse rows from the upper end of the gill slit to the base of the caudal fin is particularly distinctive in the hybrid; 41 as contrasted with 34 to 36 for the local stocks of *heteroclitus* and 44 to 51 for the Prince Edward Island *diaphanus*. The caudal ray count (branched rays plus 2) is also consistently intermediate in the hybrid. Some overlap is shown by the other scale and ray counts.

The hybrid origin of the specimen under discussion is further confirmed by a peculiar pigmentary character. Over the entire exposed surface of the scales on the top of the head there are developed, in the *F. d. diaphanus* specimens, numerous minute, seemingly melanotic tubercles. These come into clear view when the surface of the head is quickly desiccated, as by a jet of compressed air. Under this treatment the ordinary melanophores, lying deeper in the skin, become scarcely apparent (Plate III shows the melanophores and hence does not bring out the tiny, black, superficial swellings). In the examples of *F. heteroclitus macrolepidotus* these melanotic (?) structures are barely evident, and are confined to the periphery of the scale. In the hybrid they are rather well developed, but are less prominent than in the *diaphanus* material.

TABLE II

COMPARISON OF THE *Fundulus* HYBRID WITH THE PARENTAL SPECIES

Based on 15 adult females from Lake of Shining Waters, Prince Edward Island: 10 of *F. diaphanus diaphanus* (9 for the nonimbricated scale measurement), the 1 hybrid, and the 4 comparable females of *F. heteroclitus macrolepidotus* from this lake (11 adults used for the gillraker count).

	<i>Fundulus diaphanus diaphanus</i>	Hybrid		<i>Fundulus heteroclitus macrolepidotus</i>
	Range (Average)	Proportions and Counts	Hybrid Index	Range (Average)
Standard length, mm.	51.0-55.5 (53.8)	51.0		51.5-59.0 (54.1)
Thousandths of standard length				
Body depth	185-204 (195)	216	60	223-236 (230)
Caudal peduncle depth	105-117 (110)	137	67	146-154 (150)
Predorsal length	552-586 (570)	595	47	617-628 (623)
Prepelvic length	454-472 (464)	487	40	506-530 (521)
Depressed dorsal fin length	231-250 (239)	232	58	224-235 (227)
Shenfh of anal fin (height along second ray) *	0-0 (0.0)	25	47	48-57 (53)
Head depth†	163-171 (168)	178	43	184-198 (191)
Head width	150-165 (157)	173	55	181-195 (186)
Interorbital width (least fleshy)	107-114 (111)	123	55	129-137 (133)
Snout length	93-101 (97)	98	25	97-108 (101)
Orbit length	73-78 (75)	73	60	70-71 (70)
Mouth width (over-all) *	89-94 (91)	98	35	111-111 (111)
Upper lip width (transverse) *	69-75 (72)	70	29	62-68 (65)
Nonimbricated scale on top of head (maximum diameter) *	46-59 (51)	62	50	69-75 (73)
Distance between pores on top of head (Pl. III) *				
Distance A	11-22 (15)	22	87	19-27 (23)
Distance B	46-54 (49)	56	33	67-75 (70)
Distance C	21-26 (24)	20	50	14-19 (16)
Character index: A + B - C	37-48 (40)	59	53	70-86 (76)
Ratio, head depth to orbit length	2.2-2.3 (2.3)	2.5	45	2.6-2.8 (2.7)

Angle, between dorsal and ventral contours of head†	31-36 (33)	36	45	38-42 (39)
Displacement index‡	235-249 (243)	251	25	269-281 (275)
Gillraker counts	5-7 (6.0)	8	49	9-12 (10.1)
Scale counts				
Head to caudal	44-51 (48.0)	41	53	34-36 (34.8)
Predorsal scales	25-29 (26.9)	22	71	18-22 (20.0)
Dorsal origin to anal origin	16-18 (17.4)	17	18	14-16 (15.2)
On top of head (total count)	23-30 (27.6)	24	42	18-20 (19.0)
Ray counts				
Dorsal	12-13 (12.4)	12	67	11-12 (11.8)
Anal	10-11 (10.6)	10	100	10-10 (10.0)
Caudal	16-16 (16.0)	17	26	19-20 (19.8)
Pectoral	17-18 (17.2)	18	73	18-19 (18.3)
Average hybrid index, measurements, ratios, etc.				
Counts	48			
Grand average	55			
	50			

* Measured with an ocular micrometer (7 units per mm.).

† Measured vertically, below posterior end of nonimbricated scale (Pl. III).

‡ Measured with an arm protractor.

§ 10,000 times the cube root of displacement of eviscerated body in cc., divided by standard length.

|| All predorsal scales crossed by middorsal line to, but not including, the nonimbricated scale.

In general color tone (Pls. I and II) the hybrid is darker than the *F. d. diaphanus* associates, but lighter than the *F. heteroclitus macrolepidotus*. As a consequence the lateral dark bars (Pl. I) and the more or less crosswise blotching of the predorsal region (Pl. II) are of intermediate sharpness. In these features of coloration, however, there is an essential agreement with *F. d. diaphanus*. In the faint spotting of the sides, however, the approach is closer to the *heteroclitus* parental form. The blackish streak on the lower edge of the caudal peduncle in the hybrid is narrower than in *F. d. diaphanus* but broader than in *F. h. macrolepidotus*.

We regard this specimen as a very obvious hybrid, and as very consistently intermediate between its parental species.

Chriopeops goodei × *Lucania parva*

(Pls. IV-VI)

Field No. H41-12: 1 adult male (No. 1) found in a collection that was made in a shallow, diked lake and a small tributary stream, on the St. Marks Migratory Bird Refuge, just west of the Refuge fire tower, in Section 31 of Town 4 S., Range 2 E. The water here was fresh and rather clear, but brown-stained and with an organic taste. The bottom was of sand, with a little muck. *Naias marina* formed dense growths.

Field No. H41-15: 2 adult males (Nos. 2-3) obtained in a strongly brackish pond (open to the Gulf at very high tides), just east of the St. Marks Lighthouse, in Section 31 of Town 5 S., Range 1 E. The water was brown-stained, the bottom of muck and sand. The fish were seined out of reed beds filled with slimy algae.

Field No. H41-16: 1 adult female, collected along the shore of the Gulf of Mexico near the St. Marks Lighthouse, in Section 1 of Town 5 S., Range 1 W., close to the outlet of the brackish pond where collection H41-15 was made. Here the water was of almost normal Gulf salinity and moderately clear. The bottom was of soft to firm sand, with a slight growth of algae.

TABLE III

RELATIVE NUMBERS OF HYBRIDS, *Chriopeops goodei* × *Lucania parva*, AND OF THE PARENTAL SPECIES, IN COLLECTIONS FROM THE ST. MARKS MIGRATORY BIRD REFUGE, FLORIDA

	<i>Chriopeops goodei</i>	Hybrids	<i>Lucania parva</i>
Specimens in collection number			
H41-12	13	1 (male)	296
H41-13			1
H41-14			415
H41-15	18	2 (males)	344
H41-16		1 (female)	194
In collections containing hybrids	31 (3.6%)	4 (0.5%)	834 (96.0%)
In all 5 collections	31 (2.4%)	4 (0.3%)	1250 (97.3%)

These 3 collections, and 2 others, were made on April 7, 1941, on the St. Marks Migratory Bird Refuge of the Fish and Wildlife Service, with the consent and aid of Donald V. Gray, Refuge Keeper. The Refuge is on the

Gulf Coast in Wakulla County, western Florida. The area was formerly a salt marsh, but now most of the pond water is fresh because dikes have been built to keep out the sea water.

These hybrids occurred in company with an abundance of *Lucania parva* but with only a sparse population of *Chriopeops goodei* (Table III). The relative numbers for *Lucania* as given in the table are almost surely not higher, perhaps lower, than the true value for the population at the time of collection. Time did not permit picking all of the common species out of the net. The collections, however, were roughly random ones. The hybrids were not recognized in the field.

Except for Blue Springs near Marianna, farther inland, the St. Marks region is the westernmost locality from which we have collected *Chriopeops*. The 2 species have been taken together in the peninsular part of Florida, but an examination of the material fails to locate a single additional hybrid specimen. The hybrids were collected near the ecological as well as the geographical limit for *Chriopeops*, which is a more strictly fresh-water genus than *Lucania*.

When the collections listed above were sorted, the 4 *Chriopeops* $\times$ *Lucania* hybrids were separated readily from the specimens of the parental species. The features that first attracted attention lay in the distinctively intermediate coloration. How perfectly the pigmentary features of the hybrids interpose between those of the parental species is brought out by the illustrations (Pls. IV-VI) and by the following comparisons.

LATERAL DARK BAND ON BODY.—In *Chriopeops* the intense band is composed of large expanded melanophores so closely placed that their processes overlap. On the anterior two-thirds of the body this evenly colored band is confined to the lower one-half to two-thirds of the axial scale row. As the scale row immediately below is usually almost free of melanophores except at the borders, the lower edge of the band is serrate, whereas the upper border is an even line. On the caudal peduncle the band covers the lower three-fourths of the axial scale row and also darkens the upper third of the scale row beneath, producing here a smooth border on both edges. The borders of the lower two-thirds of the scale pockets of the axial row are almost jet-black—very much more heavily pigmented than is the rest of the body.

In *Lucania* the very faint band is composed of only a few small melanophores, scattered over the middle part of the scales of the axial row, so as to produce a stippled appearance, but leaving the upper and lower ends of each scale more or less free of pigment. The melanophores approach a linear arrangement. The borders of these scale pockets are very slightly blackened, or no more heavily pigmented than is the rest of the body.

In the hybrids the band is of intermediate intensity, and the large melanophores which compose it are more sparingly placed than in *Chriopeops*,

so that their processes are usually not in contact. As in *Chriopeops* the upper border of the band leaves the dorsal third of the scale light, but a few melanophores are developed here in the hybrids. The lower fifth of each axial scale pocket is either free of melanophores or much less densely stippled than elsewhere. On the caudal peduncle the melanophores of the band are mostly limited to the median half of each pocket, with a few scattered on the lower part of the pocket and on the upper fourth of the pocket below (as in *Chriopeops*). Anteriorly, the lower edge of the band shows a trace of the serration seen in *Chriopeops*. On the posterior part of the band the melanophores tend to be arranged in approximately linear rows. The borders of the axial scale pockets, especially on the dividing lines, are much more boldly blackened than in *Lucania* but less so than in *Chriopeops*.

CAUDAL SPOT.—In *Chriopeops* an intensification of melanophores on the scale pockets of the caudal base produces a jet-black spot, which varies considerably in size: its width may be slightly less than the height of 1 scale, or equal to the height of 2 scales. The spot extends from the end of the hypural plate to about the end of the scaly area on the base of the caudal. It is most intense in its anterior half; the pigmentation becomes more or less diffuse posteriorly.

In *Lucania* the lateral band ends at the hypural plate, and the scale pockets on the base of the caudal are entirely devoid of pigment except on their borders.

In the hybrids the intermediate lateral band extends to the end of the scaly sheath at the base of the caudal, widening posteriorly to the hypural plate. In 2 specimens there is an intensification of pigment on the first scale pocket behind the hypural, but in the other 2 the pigmentation here about equals that on the rest of the band.

BAND ON OPERCLE.—In *Chriopeops* the dark lateral band continues nearly straight forward to the orbit. Across the opercle it maintains the same intensity and width as on the body. Between the preopercle and the orbit the pigmentation becomes less intense and the melanophores are smaller.

In *Lucania* the very indistinct band continues forward on the opercle, bending down to meet the middle of the eye.

In the hybrids the band is of intermediate intensity and bends down slightly to meet the eye, but less so than in *Lucania*. On the opercle the intensity of the pigment is slightly greater than on the body band, but this region is less blackened than it is in *Chriopeops*.

BAND AROUND MUZZLE.—In *Chriopeops* deep-lying pigment produces a band which extends forward from the eye and around the chin, but is not developed on the lips. This mark is about as wide as the pupil. Overlying the band there is a scattering of small melanophores which extend beyond the dorsal edge of the stripe, but rarely occur below its ventral edge.

In *Lucania* a few deep-set melanophores form a suggestion of a stripe from the eye to the mouth, but there is no trace of a band on the chin. Small

superficial melanophores cover the same area between the eye and the mouth, but on the chin extend downward and backward to form a shaded area about twice as wide as the band on the mandible of *Chriopeops*.

In the hybrids the deep-lying band of pigment is situated as in *Chriopeops*, but is less intense. The overlying melanophores are fewer than in *Lucania*; they extend below the band, but not so far downward and backward as in that genus.

PREDORSAL STRIPE (Pl. VI).—In *Chriopeops* there is no trace of a predorsal stripe; the scales along the middorsal line resemble the adjoining ones in pigmentation. In *Lucania* a definite predorsal stripe extends from the origin of the dorsal fin to the occiput. In the hybrids a predorsal stripe occurs, but it is neither so wide nor so intense as it is in *Lucania*.

LIGHT STRIPE ABOVE LATERAL BAND.—In *Chriopeops* a light band 2 scale rows high lies just over the dark lateral band. In the light zone the outlines of the scale pockets are more narrowly pigmented than elsewhere, and the melanophores over the pockets are much sparser than on the scales above and below. In *Lucania* the scale pockets are evenly pigmented above the faint lateral band. In the hybrids the light band is apparent and follows the pattern of *Chriopeops*, but is not so sharply delineated as in that genus.

DARK BAND ALONG ANAL BASE.—In *Chriopeops* an intense band of black pigment extends from just above the anus to the base of the caudal fin, skirt-ing the anal base and following the mid-ventral line of the caudal peduncle. It is composed of deep-lying expanded melanophores, so closely placed that their processes are usually in contact. The bands are about one-half a scale row wide on the sides of the anal fin, and join back of the fin to cover the mid-line row of scales and the lower portions of adjacent scale pockets. In the mid-line between the anal and caudal fins there is also a conspicuous row of small melanophores, closely spaced in a single file. The borders of the band are relatively definite in the anterior portion, but become less well-defined on the caudal peduncle.

In *Lucania* there is no trace of a band along the anus and anal fin, but from the anal fin to the base of the caudal there is a row of small deep-lying melanophores, as in *Chriopeops*.

In the hybrids the bands are present, but the melanophores are more widely separated than in *Chriopeops*, so that their processes usually do not touch. The width of the band between the anal and caudal fins is about one-half to three-fourths the width of the median line of scales.

PIGMENTATION OF SCALE BORDERS BELOW AXIAL ROW.—In *Chriopeops* the pockets of the scale rows below the axial series tend to be weakly outlined by melanophores. The lower half of the first row below has a more or less well-defined edging of small or large melanophores. The second series below has the margins of the pockets poorly set off by small melanophores, or not at all pigmented, and the third row below is not outlined.

In *Lucania* the margins of the scale pockets below the lateral band are well defined. The first row beneath the axial one is sharply delineated by 2 or more marginal rows of large melanophores. The second series is always outlined by at least 1 row of large black color cells. The third row below is usually set off by a single file of well-developed melanophores, but in some specimens these are lacking. The fourth row is either poorly outlined or unpigmented.

In the hybrids the first row below the axial series has the scale pockets sharply delineated by 1 or 2 rows of large melanophores. This margining is more marked than in *Chriopeops*, but is weaker than in *Lucania*. The scale-pocket edgings on the second scale series below are weakly defined, and the third row is unpigmented.

SCALES ON TOP OF HEAD (Pl. VI).—In *Chriopeops* the scales on the top of the head are evenly pigmented, so that the borders are not sharply delineated. In *Lucania* the melanophores are concentrated toward the borders of these scales and tend to leave a light area in the center, so that the outlines stand out sharply. In the hybrids the melanophores are concentrated toward the scale borders, but the clear central area is less depigmented than in *Lucania*. The appearance is therefore intermediate.

INTERNARIAL PIGMENT SPOT (Pl. VI).—In *Chriopeops* there is a roughly triangular spot of deep-lying melanophores just in front of each posterior nostril. The base of the triangle lies between the posterior nostril and the posterior nasal pore of the lateral line system, and the apex lies between the anterior nostril and the anterior nasal pore. The melanophores are large, and their processes are in contact. In *Lucania* this spot is indistinct and contains only a few widely separated melanophores. In the hybrids it is well defined, but the melanophores are more widely spaced than they are in *Chriopeops*. Again the appearance is intermediate.

PIGMENT BELOW EYE.—In *Chriopeops* the cheek below the eye is either wholly unpigmented, or, in some males, bears a few small scattered melanophores. There is almost no tendency for a concentration of pigment along the lower border of the orbit.

In *Lucania* this region is rather well covered with large melanophores which tend to form a subocular bar, and posteriorly to line the scale pockets. There is always a concentration of pigment along the lower orbital border. In the young, in females, and in salt water there is a tendency for this pigmentation to be weaker.

In the hybrids there is more pigment below the eye than in *Chriopeops* but less than in *Lucania*. Most of the melanophores that do occur in this area are located along the lower border of the orbit.

PIGMENTATION ON BASE OF PECTORAL FIN.—In *Chriopeops* the pectoral base is either unpigmented or bears only a few small scattered melanophores. In *Lucania* there are several to many, generally large melanophores; usually enough to darken this area. Dorsally, some of these black pigment cells often

line the scale pockets. In the hybrids the pectoral base has a few rather small melanophores sometimes tending to form borders on the scale pockets.

PIGMENTATION OF EYE.—In *Chriopeops* the whole upper three-fourths of the eye is darkened, with more or less intensification in line with the lateral band. Ventrally, the dark color occurs next to the pupil, leaving a silvery crescent around the lower border of the eye (including the area where the eye of *Lucania* is crossed by a dark bar).

In *Lucania* the most prominent mark is a broad blackish bar, rarely indistinct, which extends across the cornea downward and slightly forward from the pupil. There is a similar but weaker band running upward and backward from the pupil and usually another, narrower one, extending upward and forward from the pupil. Either one or the other of the dorsal bands may be weak, and they may be scarcely evident when the whole upper part of the cornea is darkened. Commonly, there is a tendency for a silvery ring to form around the inner rim of the cornea. The area between the ventral and the posterolateral corneal bars is silvery; this silvery area may extend to the pupil, or may be separated from it by dark pigmentation.

The hybrids tend to combine the color markings of the parental species. Almost the entire cornea is blackish, becoming silvery posteroventrally. This silvery crescent is intermediate in position. The ventral dark bar of *Lucania* is rather poorly developed and hardly distinct from the dark area on either side of it; furthermore, the silvery area tends to extend into or below the position of the ventral bar. The whole upper part of the eye is so dark that only bare traces can be seen of the 2 upper dark bars of *Lucania*, and these dark bars if developed seem to be fused with the posterior and anterior darkened areas that form part of the lateral band in *Chriopeops*. There is a dark area on the cornea around the entire pupil, with a tendency for a silvery ring to form at the extreme pupillary margin.

PIGMENTATION OF DORSAL FIN IN MALES.—In *Chriopeops* the basal one-third to one-half of each interradial membrane is jet-black. Rays 1, 2, and 3 are overlain with melanophores in this basal area, but the other rays are relatively free of melanin. The border of the fin is diffusely pigmented on the interradial membranes; this color becomes intensified to black at the extreme margin.

In *Lucania* a jet-black blotch is located on the basal one-half of the front part of the dorsal fin, from the first to the third ray. This prominent mark covers the rays as well as the membranes. Distally, the pigmentation becomes somewhat less dense and is confined to the interradial membranes. The pattern of the rest of the fin is much like that of *Chriopeops*, except in that the subbasal area is dusky instead of jet-black, and the black border is less intense.

In the hybrids there is a blotch on the front of the dorsal fin, as in *Lucania*, but this mark is continued backward on the interradial membrane between the third and fourth rays. In the intensity of pigment over the rest of the fin the hybrids are intermediate between *Chriopeops* and *Lucania*.

PIGMENTATION OF ANAL FIN IN MALES.—In *Chriopeops* the basal one-third of the interradiial membranes behind ray 4 varies from dusky to jet-black; this part of the membrane between rays 1 and 3 carries no pigment, and between rays 3 and 4 the membrane is lightly pigmented. There is a narrow black band on the border of the fin, but between the 2 dark areas the membranes are unpigmented.

In *Lucania* melanophores are very sparsely distributed over all the membranes, except on the basal portions between rays 1 and 3. There is a black band on the border as in *Chriopeops*.

In the hybrids the situation is the same as in *Chriopeops*, except that the dark basal areas are much less deeply and more sparsely pigmented than in all except a few specimens of *Chriopeops*.

PIGMENTED BORDER ON THE CAUDAL FIN OF MALES.—In *Chriopeops* there is no trace of a pigmented border on the end of the caudal fin. In *Lucania*, however, the caudal has a diffusely pigmented dark border, which is composed of small scattered melanophores on the membranes and rays, and which covers approximately the posterior one-third of the fin. In the hybrids this band is developed rather weakly in one male, very slightly in another, and not at all in the third.

COLOR ON CAUDAL FIN OF MALES.—In life there is a red blotch on the basal part of each caudal lobe in *Chriopeops*. *Lucania* lacks these blotches. One of the male hybrids showed a trace of these red marks, despite the fading due to preservation for some weeks in alcohol.

OTHER CHARACTERS IN THE *Chriopeops* × *Lucania* CROSS.—In *Chriopeops* the upper and lower corners of the caudal fin are more broadly rounded than they are in *Lucania*, but the posterior edge is more abruptly truncate. In *Lucania* the posterior border of this fin forms a more regular arc. The hybrids are again intermediate (Pls. IV–V).

In *Chriopeops* the muzzle is slenderer than in *Lucania*, and the mandible is less massive and less prominent. In this respect, as in others, the hybrids are less extreme than is either parental species (Pls. IV–V).

Perhaps the most interesting character in which the hybrids are intermediate is the dentition. As its chief known generic criterion, *Chriopeops* has a regular inner row of small teeth, in addition to an outer file of large, strong teeth. In *Lucania* the teeth are strictly uniserial. The hybrids show, behind the main row, a few very small teeth obviously representing the inner row of *Chriopeops*. This is hardly the expected arrangement for a species, and is a very strong indication of hybridization.

The local race of *Chriopeops goodei* involved in the hybridization under study is a much slenderer fish than the type of *Lucania* in the same region (in some localities the local type of *Chriopeops* is as robust as the associated *Lucania*). The intermediacy of the hybrid in the depth of the body and of the caudal peduncle is brought out in Table IV. A similar situation applies to certain other proportions, as indicated in this table and in Plates IV–VI.

TABLE IV
COMPARISON OF THE *Chriopeops* × *Lucania* HYBRIDS WITH THE PARENTAL SPECIES

		<i>Chriopeops goodei</i> (P ₁)	Hybrids					<i>Lucania parva</i> (P ₂)	Difference Between Averages	Per Cent Difference†	Hybrid Index				
		(12 Males, 3-8 Females)*	Males				Female	(15 Males, 10 Females)			Males			Female	Average
			Range (Average)	No. 1	No. 2	No. 3					Average	No. 1	No. 2		
Standard length,‡ mm.	Males	25.4-31.6 (27.9)	24.9	28.0	28.7	(27.2)	33.5	25.6-29.3 (27.5)	0.4						
	Females	30.7-33.9 (32.0)						30.5-33.1 (32.3)	0.3						
1000 T.L. - 1000§	Males	206-237 (222)	253	246	244	(248)		241-282 (261)	39	18	79	56	51	} 64	
S.L.	Females	173-200 (184)					248	250-297 (275)	91	49					
Thousandths of standard length															
Body depth	Males	197-240 (219)	237	257	251	(248)		255-303 (285)	66	30	51	58	48	} 47	
	Females	195-222 (212)					236	278-306 (289)	77	36					
Caudal peduncle															
depth	Males	117-138 (130)	141	150	146	(146)		154-177 (165)	35	27	31	57	46	} 43	
	Females	109-114 (111)					131	152-174 (164)	53	48					
Head length	Males	284-297 (289)	301	300	303	(301)		298-335 (312)	23	8	52	48	61	} 48	
	Females	260-289 (273)					278	280-296 (289)	16	6					
Head width	Males	136-154 (144)	157	161	157	(158)		160-180 (169)	25	17	52	68	52	} 51	
	Females	139-146 (142)					146	151-168 (155)	13	9					
Eye length	Males	88-98 (92)	100	96	96	(97)		96-109 (102)	10	11	80	40	40	} 49	
	Females	78-86 (82)					89	97-105 (101)	19	23					
Pelvic fin length	Males	150-173 (162)	149	146	160	(152)		127-164 (146)	16	10	81	100	13	} 55	
	Females	118-137 (126)					131	137-157 (146)	20	16					
Pectoral fin length	Males	172-181 (176)	197	186	192	(192)		191-213 (202)	26	15	81	39	88	} 63	
	Females	156-171 (161)					176	177-206 (195)	34	21					
Counts															
Dorsal rays		9-12 (10.25)	12	11	11	(11.25)	11	11-13 (11.36)	1.11	11	158	68	68	68	90
Pectoral rays (both fins)		23-27 (24.50)	26	26	26	(26.0)	26	24-30 (26.88)	2.38	10	63	63	63	63	63
Scales, head to caudal		29-30 (29.55)	28	28	28	(28.0)	28	25-27 (26.24)	3.31	11	47	47	47	47	47
Scales, around body¶		18-20 (19.65)	20	22	20	(20.5)	20	20-23 (21.96)	2.31	12	15	102	15	15	37
Averages (measurements)									35	22	63	58	50	38	52
Averages (counts)									2.28	11	71	70	48	48	59
Grand averages											66	62	49	42	55

* 3 females measured, 8 counted.

† As compared with the figure for *Chriopeops goodei*.

‡ Specimens of parental species were selected to match the hybrids in size (for the measurements).

§ Relation between total length and standard length.

|| Averages for counts apply to both sexes.

¶ Counted from first scale in front of dorsal downward and forward to mid-line of belly, then upward and backward to the point of origin.

The interjacency of the hybrids between the local stocks of the parental species is also indicated by the counts of dorsal and pectoral rays and of scales (Table IV), despite the fact that the meristic differences between the parents are slight. The average hybrid index for the measurements is 52, for the counts, 59, for both measurements and counts, 55—a deviation of only 10 per cent from an indication of exact intermediacy.

When all this cumulative evidence is considered, it can hardly be questioned that *Chriopeops goodei* and *Lucania parva* occasionally hybridize, to produce offspring that are wonderfully intermediate between the parental species.

Fundulus sciadicus × *Plancterus kansae*

U.M.M.Z. No. 135141: 1 half-grown fish, collected by Raymond E. Johnson and Paul Romberg in the South Platte River, 2 miles northeast of the Colorado state line, in Deuel County, Nebraska, on July 21, 1940.

TABLE V
RELATIVE NUMBERS OF HYBRIDS, *Fundulus sciadicus* × *Plancterus kansae*, AND
OF THE PARENTAL SPECIES

Specimens from the Platte Rivers (Excluding Tributaries)	<i>Fundulus sciadicus</i>	Hybrids	<i>Plancterus kansae</i>
Specimens in random collection No. 266	4 (0.7%)	1 (0.2%)	554 (99.1%)
In collections (some not random) con- taining both species	291 (27.4%)	1 (0.1%)	769 (72.5%)
In all Platte River collections	301 (16.7%)	1 (0.1%)	1501 (83.3%)

When this hybrid was collected the South Platte River was reduced to a series of isolated pools in a broad, coarse-gravelled bed. Each pool was about 20 feet in diameter and 2 feet deep, with a bottom of fine sand and soft muck. There was a slight current caused by a subsurface flow between the pools. The relative coolness of the water (76° F.) was due in part to that factor and in part to the deep shade furnished by a very thick mat of *Spirogyra* and by cottonwood and willow trees growing on the higher gravel ridges in the stream course.

An attempt was made to seine and preserve in formalin every fish present in 1 pool. In addition to the 1 hybrid, 23.4 mm. in standard length, there were obtained 4 examples of *Fundulus sciadicus* 20 to 29 mm. long, 554 specimens of *Plancterus kansae* 16 to 61 mm. long, 4 thriving young of *Pimephales promelas promelas*, and 2 emaciated adults of *Notropis dorsalis dorsalis* × *piptolepis*. In Nebraska *Fundulus sciadicus* occurs mainly north of the Platte River and *Plancterus kansae* south of that river. The 2 genera meet and occur together only in the North and South Platte rivers proper. *Fundulus sciadicus* was very seldom found in abundance at any point in those streams, and was greatly outnumbered by *Plancterus kansae*

at most places where the 2 species were seined together. A careful check of all the Platte River material failed to uncover another hybrid.

The systematic and nomenclatorial status of these cyprinodonts, the only species of the family known from Nebraska, has been treated by Hubbs (1926: 10-11, 15).

Despite its small size the peculiar cyprinodont specimen from the Platte River displays characters by which it is readily diagnosed as an interspecific hybrid. Attention was first attracted to this fish when it was seen to combine the vertical bars of *Plancterus kansae* with the rather uniform brassy to reddish olive undertone, overlain with minute brownish flecks, of *Fundulus sciadicus*. *Plancterus kansae* contrasts sharply with *Fundulus sciadicus* in being greenish above, yellowish on the sides, and almost white below. Its sides are crossed by 12 to 18 prominent vertical dark bars, extending from the head to the caudal fin. The Plains species of *Fundulus* never has a trace of these cross bars. The hybrid shows 8 to 10 of the cross bands, almost hidden by the uniform dark undertone.

A closer scrutiny of the pigment disclosed other, equally distinctive features of the parental species, which are blended in the hybrid. In *Fundulus sciadicus* small melanophores are very evenly dusted over the dorsal and lateral scales and form a pattern of fine pepper marks around the front of the muzzle. In *Plancterus kansae* the melanophores are larger. Those on the back and upper sides are loosely clumped into pigment spots that tend to be concentrated on the posterior field of each dorsal and lateral scale, leaving the intervening spaces clear. Around the muzzle the melanophores are larger and less densely spaced. In these characters the hybrid is intermediate, possibly favoring the *Plancterus* parent in the pigmentation of the dorsal scales. The *Fundulus* displays a prominent middorsal dusky stripe, which extends with uniform intensity from the occiput to the dorsal fin. In *Plancterus* the predorsal stripe is restricted to a distinct black diamond-shaped spot just in advance of the origin of the dorsal. The hybrid possesses a diamond-shaped mark at the same point, but this spot is elongated into a stripe extending halfway to the occiput.

The *Fundulus* has very little pigment on the interradiar membranes of the pectoral fin. Only a few minute flecks show faintly near the fin margin, but elongated melanophores in 1 series form a sharp, black outline along the full length of the upper and lower border of each ray. In *Plancterus*, on the other hand, the pigment cells are scattered widely over the membranes and do not form a definite border along the sides of the rays. The hybrid resembles the *Fundulus* parent in having each pectoral ray outlined with black, but the pigmentation is very weak and in places the outline is broken.

In view of the wide differences between the presumed parental species in the number of scales and fin rays, the supposition that the aberrant

species is a hybrid was tested by counting the meristic features. Four ray counts and 4 scale counts were taken on the hybrid and on 15 specimens of each parental species. As was expected the counts proved to be almost exactly intermediate (Table VI, lower part). Each value for the hybrid intervened between the corresponding counts for the parental species, when the figures were widely divergent, and agreed with the adjacent extreme count of the one or the other type, when the ranges for the parents were barely separated.

Since all of the scale enumerations and all of the fin counts except the caudal ray number were found to be definitely higher in the *Plancterus* than in the *Fundulus*, it is obvious that the distinction between the species can be emphasized by a character index: the number of caudal rays subtracted from the sum of all 7 other counts for each individual. A gap of 97 points separates the index values for the 2 species, and the figure for the hybrid lies nearly midway between:

Character index for scale and ray counts:

<i>Fundulus sciadicus</i>	127 to 141 (average, 132)
Hybrid	173
<i>Plancterus kansae</i>	221 to 241 (average, 229)

The hybrid index for this character index is 42.

Similar intermediacy is also shown for the critical measurements (Table VI, upper part). In several proportions the approach is greater toward the *Plancterus* than toward the *Fundulus* parent. The average hybrid index of 62 for the measurements, however, very strongly confirms the identification of the specimen as a hybrid. The grand average hybrid index of 55, for all counts and measurements, is only 10 per cent higher than the value of exact intermediacy, and happens to be identical with the similar value obtained for the *Chriopeops* $\times$ *Lucania* crosses.

The position of the dorsal fin is brought out not only by the proportionate measurement of predorsal length (Table VI) but also by the relation of the dorsal to the anal fin. In *Fundulus sciadicus* the front end of the dorsal fin lies distinctly behind the origin of the anal fin. *Plancterus* has the insertion of the dorsal fin ahead of the anal origin. In the intermediate hybrid the origins of the 2 fins are on about the same vertical.

The caudal fin of the hybrid shows an intermediate feature in the curvature of the posterior border, which is neither as rounded as in the *Fundulus* nor so truncate as in *Plancterus*. Probably because of its youth or its condition of preservation, the hybrid does not display interjacency in the degree of fanning out of the caudal fin (which is greater in the *Fundulus* than in the *Plancterus*).

The hybrid also intervenes between the parental forms in the position and structure of the pelvic fins. In this respect the 2 species are quite distinct. In the *Fundulus* the pelvics are inserted very close together and

are conjoined at their bases by a large sheath of skin. The *Plancterus* pelvises are separated by a distance almost as great as the width of the base of either fin, and no dermal fold binds their proximal halves together.

The gill-rakers also proclaim the specimen to be a hybrid. In *Fundulus sciadicus* these structures are short and on the lower part of the arch become rudimentary tubercles. Even anteriorly *Plancterus* has long, slender, and curved rakers. In the hybrid they are rather long, but on the lower part of the arch are definitely shorter, almost knoblike.

TABLE VI
COMPARISON OF THE *Fundulus* × *Plancterus* HYBRID WITH THE PARENTAL SPECIES

	<i>Fundulus sciadicus</i>	Hybrid		<i>Plancterus kansae</i>
	(10 Measured, 15 Counted)	Proportions and Counts	Hybrid Index	(10 Measured, 15 Counted)
	Range (Average)			Range (Average)
Standard length, mm.*	20.1-29.1 (24.5)	23.4		22.0-24.1 (23.1)
Thousandths of standard length				
Predorsal length	670-700 (688)	674	21	590-643 (622)
Body depth	231-261 (250)	218	68	195-213 (203)
Caudal peduncle depth	149-168 (158)	128	68	109-123 (114)
Head depth	189-203 (196)	184	86	177-188 (182)
Snout length	97-107 (103)	107	80	100-111 (108)
Eye length	75-94 (87)	81	50	70-77 (75)
Anal fin, depressed length	219-258 (237)	222	58	204-230 (211)
Counts				
Dorsal rays	9-10 (9.1)	12	51	14-16 (14.8)
Anal rays	11-12 (11.5)	13	68	13-15 (13.7)
Principal caudal rays	16-19 (17.9)	16	49	13-15 (14.0)
Pectoral rays	14-15 (14.2)	15	40	16-17 (16.2)
Scales, lateral line	33-40 (35.9)	47	39	59-69 (64.5)
Scales, around body†	30-36 (32.6)	43	38	57-66 (60.3)
Scales, around peduncle	18-21 (19.8)	25	51	28-33 (30.0)
Scales, predorsal	21-25 (23.1)	30	64	36-43 (39.9)
Average hybrid index, measurements			62	
counts			50	
Grand average			55	

* Specimens of the parental species were selected to match the hybrid in size.

† Counted vertically around body just in front of the pelvic fins, in a zigzag line.

The hybrid is interposed between *Fundulus* and *Plancterus* in at least one of the generic differences (Hubbs, 1926: 14). In *Fundulus* the gill-opening is free to the angle of the opercle, and the slit therefore extends far above the upper end of the pectoral base. In *Plancterus* the upper part of the opercle is bound down to the shoulder girdle, so that the slit extends upward only to about opposite the uppermost pectoral ray. The hybrid is nicely intermediate. The other assigned generic differences (length and convolution of the intestine, and the strength and shape of the pharyngeal teeth) were not investigated, because of the small size of the one hybrid specimen.

CONCLUSIONS

The family Cyprinodontidae is now added to the list of fish groups in which species are known to hybridize in nature. We write "known to hybridize" advisedly, because in our judgment the circumstantial evidence for natural hybridization in this family, in conjunction with the data for other groups, is reliable and conclusive. The basis for interpreting certain specimens as interspecific hybrids has recently been outlined (Hubbs, Hubbs, and Johnson, 1943: 11-14), and need not be repeated here.

The three cyprinodontid hybrids now described lie between *Fundulus diaphanus diaphanus* and *Fundulus heteroclitus macrolepidotus*, between *Chriopeops goodei* and *Lucania parva*, and between *Fundulus sciadicus* and *Plancterus kansae*. *Fundulus heteroclitus macrolepidotus* is chiefly marine; the race of *Lucania* involved ranges from salt to fresh water; the other species are fresh-water fishes. The principle that fresh-water forms are more subject to hybridization than are marine fishes is thus extended.

Natural hybridization between species in the Cyprinodontidae must be one of the rarest of phenomena. The discovery would not likely have been made, had it not become a custom in ichthyological field work to collect and preserve large series of specimens.

As usual the new fish hybrids prove more or less exactly intermediate between the parental forms, in the various characters by which the species are distinguishable. The features in which the cross-bred individuals intervene between the parental species are deep-seated as well as superficial. In two of the three combinations there are involved structures so trenchantly different as to be regarded as of generic significance, along with details of pigmentation. The *Fundulus* $\times$ *Fundulus* hybrid exhibits intermediacy in such features as the pattern formed by the pores and canals on the top of the head, the height of the anal sheath at the side of the oviducal pouch, and the volume of the eviscerated body. There are differences, too, in meristic counts and in measurements. In brief, the hybrids are intermediate in the whole complex that makes up the "different reaction systems" of the parental species. On the percentage scale in which the values for the characters of one parental species are set at 0 and that for the other species at 100, the degree of intermediacy of the three hybrids under discussion is expressed by the grand average hybrid index of 50 for the cross between species retained in *Fundulus* and 55 for each of the crosses regarded as intergeneric.

The three cyprinodont hybrid combinations agree in another respect, namely, that the only known hybrids have been taken where only a few fish of the one parental species occur with an abundance of the other parent (Tables I, III, and V). That the association of a rare and an abundant species is conducive to hybridization has been indicated a number of times. Most of the pertinent evidence has not been published, but two outstanding cases of this phenomenon were discussed in the recent paper on catostomid

hybrids (Hubbs, Hubbs, and Johnson, 1943: 39, 48). Apparently, the very rare species may often or even usually be forced to miscegenate with the abundant species.

If most interspecific hybridization leads to sterility and hence to biotic inefficiency, as we assume it does, the tendency of species to hybridize where they are rare may well be an adverse factor in survival in the periphery of their ranges, and hence in their dispersal. Local extirpation of the rare form might thus be accelerated, as Greene (1935: 87-89) has suggested for local populations of the cyprinid fish *Clinostomus elongatus*. Ranges might thus be limited, and complementary distributions of related species built up and maintained. If, as is now generally conceded, a small advantage may lead to the spread of a gene through a population, it must be granted that a small loss in biotic potential, induced through occasional hybridization, might in time have a deleterious effect in dispersal and survival. We assume, however, that hybridization would ordinarily be only a contributing factor in limiting the range of a species or the life of a local population.

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PLATE I

Hybrid cyprinodont, *Fundulus diaphanus diaphanus* $\times$ *Fundulus heteroclitus macrolepidotus*, and the parental species

All from Lake of Shining Waters, Prince Edward Island, Gulf of St. Lawrence.
Photographed to the same scale by Clarence Flaten.

FIG. 1. *Fundulus diaphanus diaphanus*, female.

FIG. 2. Female hybrid, 51 mm. in standard length.

FIG. 3. *Fundulus heteroclitus macrolepidotus*, female.



PLATE II

Dorsal view of hybrid cyprinodont, *Fundulus diaphanus diaphanus* $\times$ *Fundulus heteroclitus macrolepidotus*, and of the parental species

All from Lake of Shining Waters, Prince Edward Island, Gulf of St. Lawrence. Same specimens as shown in Plate I. Photographed to the same scale by Clarence Flaten.

FIG. 1. *Fundulus diaphanus diaphanus*, female.

FIG. 2. Female hybrid, 51 mm. in standard length.

FIG. 3. *Fundulus heteroclitus macrolepidotus*, female.

3

2

1



PLATE III

Dorsal view of head of hybrid cyprinodont, *Fundulus diaphanus diaphanus*
× *Fundulus heteroclitus macrolepidotus*, and of the parental species

All from Lake of Shining Waters, Prince Edward Island, Gulf of St. Lawrence. Same specimens as shown in Plates I and II. Photographed to the same scale by Clarence Flaten; retouched to emphasize sensory pores and the nonimbricated scale. A, B, C are distances measured by eye-piece micrometer and used in computing a character index.

FIG. 1. *Fundulus diaphanus diaphanus*, female.

FIG. 2. Female hybrid, 51 mm. in standard length.

FIG. 3. *Fundulus heteroclitus macrolepidotus*, female.



PLATE IV

Hybrid cyprinodont, *Chriopeops goodei* $\times$ *Lucania parva*, and the parental species

All from St. Marks Migratory Bird Refuge, Florida. Photographed to the same scale by Clarence Flaten.

FIG. 1. *Lucania parva*, male, from collection H41-15.

FIG. 2. Male hybrid, 28.7 mm. in standard length, from same collection.

FIG. 3. *Chriopeops goodei*, male, from same collection.



PLATE V

Hybrid cyprinodont, *Chriopeops goodei* $\times$ *Lucania parva*, and the parental species

All from St. Marks Migratory Bird Refuge, Florida. Photographed to the same scale by Clarence Flaten. Owing to the bright illumination required in taking this picture, the melanophores on the lower part of the head are scarcely apparent.

FIG. 1. *Lucania parva*, female, from collection H41-16.

FIG. 2. Female hybrid, 33.5 mm. long, from same collection.

FIG. 3. *Chriopeops goodei*, female, from collection H41-15.



PLATE VI

Dorsal views of head and nape of hybrid cyprinodont, *Chriopeops goodei*
× *Lucania parva*, and of the parental species

All from St. Marks Migratory Bird Refuge, Florida. Photographed to the same scale
by Clarence Flaten.

FIG. 1. *Lucania parva*, male, from collection H41-15.

FIG. 2. Male hybrid, 28.7 mm. in standard length, from same collection.

FIG. 3. *Chriopeops goodei*, male, from same collection.



